FOOD SIZE, FOOD TYPE, AND FORAGING SITES OF RED-WINGED BLACKBIRDS

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Before the onset of the breeding season, Red-winged Blackbirds (*Agelaius phoeniceus*) shift from an herbivorous to an insectivorous diet (Hintz and Dyer 1970). Morton (1973) suggested that such seasonal changes in feeding are important in providing a high protein diet for rapidly growing nestlings. During the time nestlings are being fed, both quality and quantity of food are critical for rapid growth.

Feeding efficiency, the maximizing of the number of calories delivered to the nestlings per unit time, is important because the parent birds are limited in the number of feeding trips they can make per day. One method of increasing feeding efficiency may be selection of the largest food items relative to the time and energy expense of capture. Smaller insects are ordinarily more abundant than larger insects and either obligate selection of only large insects or random selection of all insects might be energetically inefficient. Nevertheless, one might expect a shift to the larger size spectrum with the sizes selected a function of energy expended in search and capture (Emlen 1966). In this regard, Hespenheide (1966) noted that some species of birds do choose the largest food items in relation to energy expended. Wilson (1975) noted that, within specified limits, success of prey capture increases with an increase in prey size. Feeding efficiency might also be increased by selection of specific food types such as slow-moving insect nymphs and larvae.

Another method of increasing feeding efficiency may be by reduction of competition, especially intraspecific competition. If different segments of the population, for example different age classes or sexes, foraged in a dissimilar manner or in different locations, competition might decrease, leading to an increase in foraging efficiency. Many authors (e.g., Selander 1966) have shown that males and females in many sexually dimorphic species forage at different sites on essentially different prey populations.

The purpose of this study was to evaluate the importance of food size, food type, and foraging sites in relation to the feeding efficiency of Red-winged Blackbirds while feeding nestlings. The study consisted of determining: (1) the size of food items fed nestlings versus the sizes potentially available, (2) the developmental stage of the food eaten, and (3) the importance of intraspecific competition for food during the breeding season.

MATERIALS AND METHODS

Red-wings were studied at a marsh (ca 3 ha) and adjacent field (ca 3 ha) on the north shore of Lake Springfield, 3.2 km south of Springfield, Missouri. Dominant vegetation in the marsh consisted of cattails (*Typha latifolia*), water willow (*Justicia americana*), bulrush (*Scirpus lineatus*), arrowhead (*Sagittaria latifolia*), cutgrass (*Leersia* sp.), and black willow (*Salix nigra*). Grasses were dominant on the field which, during the summer, was mowed bi-weekly.

I collected food samples from 3-to-8-day old nestlings, using Orians' (1966) pipe-cleaner, neckcollar technique, between 08:00 and 11:00 (CDT) on alternate days from 27 May to 5 June and from 20 June to 4 July 1974. This time period was chosen to keep the data consistent and to prevent starving the nestlings, thus adding a possible bias. Each food sample represented 1½ to 2 h of food delivery. Thirty samples representing ca 53 h of feeding time were collected. Food items were identified to family (when possible) and length measured to the nearest 0.5 mm.

Sweepnet samples were taken at 5 stations, 3 on the field and 2 on the marsh, every 2 to 3 days between 08:00 and 11:00 from 27 May to 8 July 1974. Each sample was composed of 10 sweeps with a heavy-duty sweepnet scraping the ground and vegetation just above the ground. The purpose of the sweepnet samples was to obtain an index to the size distribution of organisms a bird might encounter if feeding were random within these habitats. It is unlikely that an individual bird would encounter this full range of sizes at all times and in all places. Nevertheless, the sweep samples serve as a measure of potentially available prey size distribution. Janzen (1973) felt that the composition of insects collected by sweep sampling and actually present in the foliage was in general agreement.

Foraging activity data were gathered on the field because dense vegetation prevented similar observations on the marsh. Birds foraging on the field were observed for a 90 min period between 08:00 and 11:00 every 2 to 3 days from 27 May to 9 July 1974 for a total of 30 h. Any bird exhibiting feeding behavior, either on or within ca 1.5 m of the ground, was counted as feeding. The number of male and female Red-winged Blackbirds on the field was recorded at 10 min intervals for the 90 min period in the manner of Austin and Smith (1972).

RESULTS

Comparison of the number of male and female Red-winged Blackbirds foraging on the field with the number expected (if male and female population sizes were equal) by the G-test (Sokal and Rohlf 1969) indicated a significantly higher use of the field by males than by females ($P < 0.005$: Table 1). The males that foraged on the field consisted of breeding and possibly a few non-breeding individuals. Two population censuses were made along the periphery of the marsh; 14 males and 14 females were counted on 20 June and 13 males, 13 females were counted on 18 July 1974. As males were more conspicuous than females (e.g., calling on their territories), the number of females was probably underestimated. Furthermore, females generally outnumber males in Red-winged Blackbird breeding populations, which strengthens the conclusion that males are selecting the field on which

TABLE 1
NUMBER AND PROPORTIONS OF MALES AND FEMALES FORAGING ON THE FIELD

Date	Number* of males	Number* of females	Ratio of females/males
May 27	20	5	0.25
28	19	5	0.26
June 1	47	5	0.11
3	49	3	0.06
12	38	7	0.18
14	17	2	0.12
17	44	1	0.02
19	46	0	0.00
21	27	3	0.11
25	2	0	0.00
28	24	0	0.00
29	17	3	0.18
30	13	0	0.00
July 2	35	1	0.03
4	71	3	0.04
9	54	1	0.02
Total	523	39	0.07
$\bar{x} \pm SE$	32.7 ± 1.92	3.0 ± 0.48	

* Sum of the number of males and females observed in each 10 min time period for the 90 min observation period.

to forage (Haigh 1968, Dolbeer 1976). In any event, in order for these data (Table 1) to be a simple reflection of an unbalanced sex ratio, the population would have to consist of at least 91% males ($P > 0.05$) for even if the population consisted of 90% males, which is unlikely, there would still be a significant difference between observed and expected male/female activity on the field ($P < 0.01$).

Because males and females appeared to forage in different locations, the sizes of potential prey organisms in 2 probable foraging areas, the field and marsh, were compared. Mann-Whitney U-test analysis indicated that the average size of organisms I caught on the marsh was significantly larger than the average size of organisms caught on the field (Table 2). Furthermore, 2-way analysis of variance revealed that the mean body length of representatives of 8 orders of arthropods on the marsh were larger than those on the field ($P < 0.001$), that the average length of representatives of the orders differed significantly ($P < 0.001$), and that there was no significant interaction between location and taxa ($P > 0.10$; Table 2). Because sample sizes were unequal, randomly selected subsamples of equal size were taken

TABLE 2

MEAN BODY LENGTH OF ARTHROPODS CAPTURED IN THE FIELD AND MARSH

Order	Field			Marsh		
	N	Mean ± SE (mm)		N	Mean ± SE (mm)	
Collembola	227	0.60	0.171	39	0.76	0.254
Orthoptera	32	5.09	0.297	258	7.97	0.328
Hemiptera	98	3.9	0.33	21	6.2	0.95
Homoptera	639	3.0	0.30	345	3.7	0.41
Coleoptera	130	3.4	0.39	135	4.9	0.42
Diptera	711	2.63	0.255	654	3.16	0.239
Hymenoptera	108	2.11	0.263	39	3.3	0.34
Araneae	63	2.8	0.36	73	3.0	0.43
All Organisms*	2063	2.76	0.139	1685	4.79	0.188

* Includes arthropods and other organisms.

for each of the categories (i.e. 21 samples from the Collembola captured on the field, where $N = 227$; 21 samples from Orthoptera captured on the field, where $N = 32$, etc.). These data were transformed to their common logarithms and then analyzed.

Comparison of the size frequency of potentially available prey organisms with nestling food samples by the Mann-Whitney U-test showed that nestlings were fed significantly larger items ($P < 0.001$) than were potentially available (Fig. 1). Because potential prey organisms in the marsh were significantly larger than those in the field and in order to test whether the size frequency difference between nestling food and sweepnet samples was due to sampling location, I compared the size frequency distributions of marsh organisms and nestling food samples (Fig. 1). Mann-Whitney U-test analysis revealed that nestling food organisms were significantly larger than potential prey from the marsh ($P < 0.001$).

In order to evaluate the type of prey in terms of insect developmental stage fed to nestlings, I compared the sizes and frequency of occurrence of adult, nymphal, and larval insects captured in the marsh and fed to nestlings. All non-insect arthropods appeared to be adults and, for purposes of analysis, were counted as such.

Mean body lengths of organisms captured by sweepnet sampling in the marsh and taken from nestlings for each of 3 insect developmental stages (adults, nymphs, and larvae) are compared in Table 3. Two-way analysis of variance of these randomly selected, equal-sample-sized, log-transformed data (see above) indicated: (1) a significant difference in size between what was
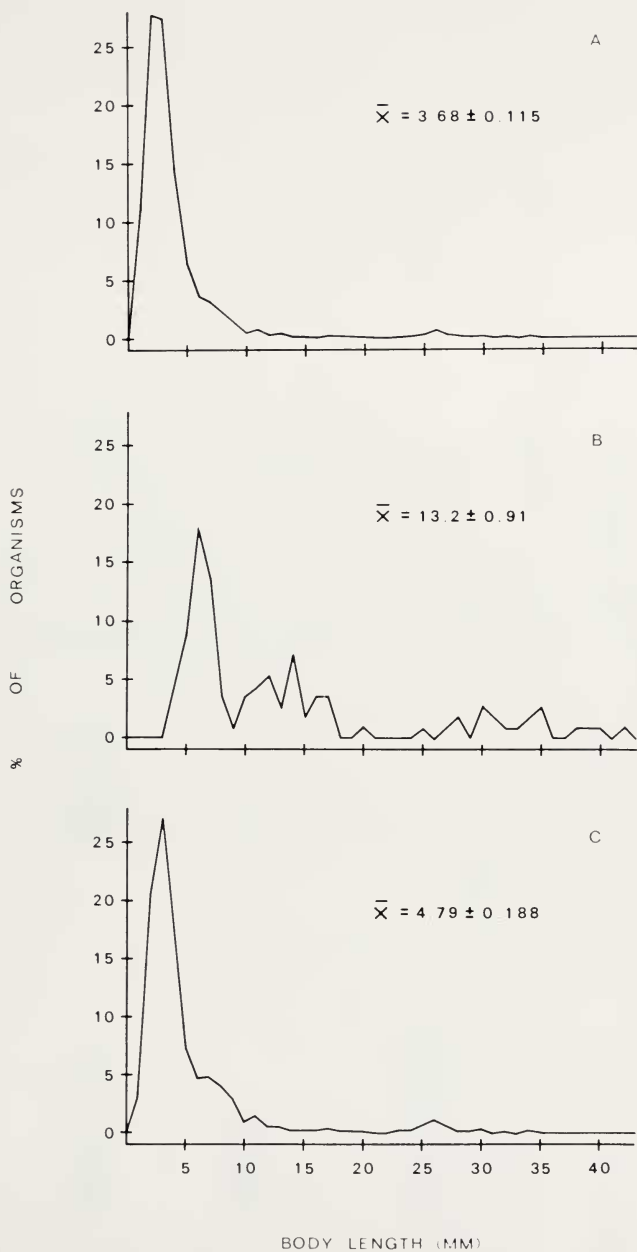
FIG. 1. Percent of body lengths of sweepnet samples and nestling food samples. A. Combined marsh and field sweepnet samples, N = 3768. B. Nestling food samples, N = 112. C. Marsh sweepnet samples, N = 1685. x̄ = mean ± standard error.

TABLE 3

MEAN BODY LENGTH OF ADULTS, NYMPHS, AND LARVAE TAKEN FROM
NESTLINGS AND CAPTURED BY SWEEPNET SAMPLING ON THE MARSH

Developmental Stage	Nestling Food Samples			Marsh Samples		
	N	Mean ± SE (mm)		N	Mean ± SE (mm)	
Adults	44	19.0	1.82	1291	4.35	0.231
Nymphs	25	10.5	2.00	368	6.34	0.263
Larvae	38	8.2	2.08	11	6.2	0.84

fed nestlings and what prey organisms were potentially available ($P < 0.005$), (2) no significant difference among the sizes of developmental stages ($P > 0.5$), and (3) a significant interaction among developmental stages within the sweepnet samples and nestling food samples ($P < 0.05$).

If the nestlings are fed items selected at random, the percentage of adults, nymphs, and larvae fed to the nestlings should correspond to the percentage of adults, nymphs, and larvae occurring in the feeding area (Fig. 2). However, a G-test of arcsine-transformed data indicated that there was a signifi-
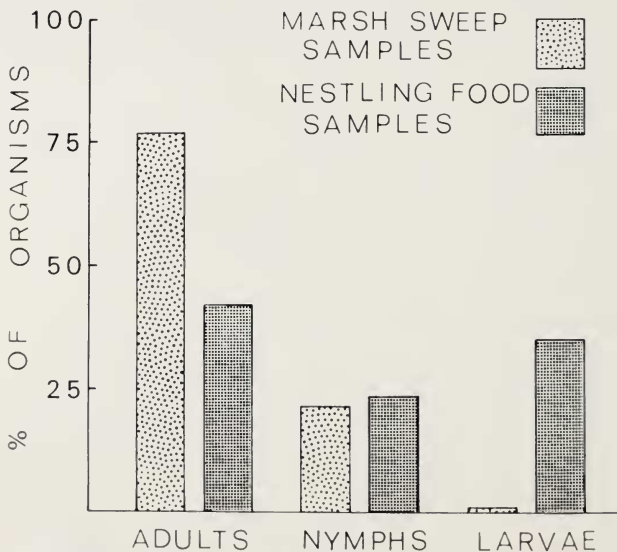

FIG. 2. Percent of developmental stages of marsh sweepnet samples and nestling food samples. Marsh samples, N = 1685; nestling food samples, N = 107.

cantly higher proportion of nymphs and larvae in the nestlings' diets than in the marsh sweepnet samples ($P < 0.005$).

<div align="center">DISCUSSION</div>

The observation that male Red-winged Blackbirds used the field as a foraging site significantly more often than females suggests a sexual difference in foraging site preference. Selander (1966) noted that male and female Red-winged Blackbirds have been observed feeding in sexually segregated flocks in the fall, but to my knowledge this has never been observed during the breeding season. After 216 h of observation during the breeding season, Brenner (1968) noted that females were never seen feeding off the marsh. I observed few females feeding on the field (Table 1), but many feeding in the marsh.

The importance of sexual differences in foraging sites can be related to the role of the female in feeding nestlings. Verner and Willson (1969) indicated that males do not generally feed nestlings. If a strict time-energy budget exists for the female in feeding nestlings, then any mechanism that may reduce competition for food would be advantageous. Even a slight segregation of foraging sites at a critical time (such as during nestling feeding) may reduce intraspecific competition for food.

In addition to the observation that females fed significantly less often in the field than did males, and that one probable female feeding area was the marsh, I noted that these locations offer significantly different-sized prey organisms. Comparison of the arthropod faunas of the marsh and field indicated that the average size of organisms occurring in the marsh was larger than that of those on the field. Hence, the marsh was likely a more "profitable" place to forage in terms of the number of calories per organism than the field.

That prey items fed to nestlings differed significantly in size from what was potentially available can also be related to the role of the female in feeding nestlings. During the first 9 days of life, nestling weight increases ca 700% (Robertson 1973). Using the existence-energy equations of Kendeigh (1970) and Wiens and Innis (1974), a 43.5 g female Red-winged Blackbird (an average of 10 specimens from the University of Oklahoma collection) would require ca 32.6 kcal day^{-1} and a nestling would require ca 147 kcal during the first 9 days after hatching (nestling weight data from Robertson 1973). These results are similar to those found by Brenner (1968) and Haigh (1968). The average size of items fed to nestlings in my study was 13.2 mm (Fig. 1). Orians (1973) estimated that a 13 mm orthopteran contains about 50 cal. Thus, accepting these assumptions, during the first

9 days, a parent bird would have to deliver ca 2940 "average-sized" items per nestling. This tends to support the contention that a strict time-energy budget exists for the female while feeding nestlings.

From an energy standpoint, it would be advantageous to ignore smaller and/or fast-moving food items and to feed on larger and/or slower moving food items (i.e. dragonfly tenerals, insect larvae, etc.). Comparison of the frequency size distributions of the prey fed to nestlings and the prey potentially available to nestlings (Fig. 1) supports the contention that small prey items are ignored. Both distributions seem to reflect log-normal distributions as found by Schoener and Janzen (1968), but with a shift to larger sizes in the nestling prey distribution.

The apparent selection for larvae and nymphs might be attributed to their soft anatomy, their ease of capture, or both. Pulliam (1975) postulated that animals may show partial preferences in feeding when nutrient constraints exist. Also, rapid assimilation of nutrients would favor rapid growth, and selection for softer food items could be an evolutionary response to the necessity for rapid food breakdown. Furthermore, a larva, nymph, or an emerging adult is easier to capture than a flying adult. Nevertheless, some hard insect parts are necessary for the mechanical breakdown of food (Bird and Smith 1964). West (1973) noted similar feeding patterns in Tree Sparrows (*Spizella arborea*). Alcock (1973) indicated that Red-winged Blackbirds have the ability to distinguish food items on the basis of visual and locational cues.

Two mechanisms, a tendency for males to feed in an area little used by females and a tendency for females to feed nestlings relatively large and soft food items, may be related to the role of the female in feeding nestlings and to the females' strict time-energy budget as a result of having to feed rapidly growing nestlings unassisted. A female has the capability of making only so many feeding trips per day. If the number of trips per day is roughly constant, then the more calories of food brought to the nestlings per trip, the higher the probability that the young will be adequately nourished throughout the nestling period. A female could satisfy this food demand by bringing many small prey items per trip instead of a few larger items. However, it is unlikely that many small items can be gathered with less expenditure of time and energy than the same biomass represented by one or several larger, slower moving items unless the small items were highly clumped and constantly available which is unlikely to occur very often. Bird and Smith (1964), Snelling (1968), Hintz and Dyer (1970), and Voigts (1973) indicate that Red-winged Blackbirds feed on a wide variety of prey, which supports the contention that generally the birds do not exclusively use small, highly clumped prey.

SUMMARY

Female Red-winged Blackbirds were found to feed less often on the field than were males; this may reduce intraspecific competition. The average size of organisms captured by sweepnet sampling in the marsh, the area in which females possibly fed, was significantly larger than on the field.

The size of organisms fed to nestlings was significantly larger than if food selection were random. There was also an apparent preference for soft-bodied items. As females feed nestlings unassisted by males, time-energy budget constraints make it necessary for females to maximize feeding efficiency. Preferences in food size, food type, and foraging locations may serve to do this.

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